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Reassessment of the systematics of the widespread Neotropical genus *Cercomacra* (Aves: Thamnophilidae)

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A comprehensive molecular phylogeny of the family Thamnophilidae indicated that the widespread neotropical genus *Cercomacra* Sclater, 1858 is polyphyletic. Two non-sister clades in putative *Cercomacra* were uncovered: (1) the '*nigricans*' clade (*Cercomacra sensu stricto*), formed by *manu*, *brasiliana*, *cinerascens*, *melanaria*, *ferdinandi*, *carbonaria*, and *nigricans*; and (2) the '*tyrannina*' clade formed by *nigrescens*, *laeta*, *parkeri*, *tyrannina*, and *serva*. *Sciaphylax* was sister to the '*tyrannina*' clade and this group was sister to a clade formed by *Drymophila* and *Hypocnemis*. This whole major clade then was sister to *Cercomacra sensu stricto*. Further work is needed to resolve the phylogenetic placement of *brasiliana* and *cinerascens* within *Cercomacra*, and the relationships within the '*tyrannina*' clade. Because the group of species referred to as the '*tyrannina*' clade does not have an available name, we erect a new genus that recognizes the monophyly and distinct nature of this group. A molecular time scale for the evolution within *Cercomacra sensu lato* is proposed.

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ADDITIONAL KEYWORDS: CYTB – FIB5 – ND2 – ND3 – phylogenetics – Pithyini – polyphyly – taxonomy.

INTRODUCTION

Our ability to understand the evolution of the high biological diversity of the Neotropics relies on accurate systematics and taxonomy. The ability to use molecular data to assess phylogenetic relationships is leading to new insights that are overturning relationships in many lineages of Neotropical organisms. One of these lineages, the typical antbirds (Thamnophilidae), comprises the largest group within the tracheophone assemblage of New World suboscines (Irestedt *et al*., 2002, 2004; Brumfield *et al*., 2007; Moyle *et al*., 2009; Ohlson *et al*., 2013). This highly diverse Neotropical family includes 220 species in at least 48 genera of insectivorous forest birds distributed from southern Mexico to Paraguay and northern Argentina (Zimmer & Isler, 2003; Remsen *et al*., 2013). Antbirds represent a significant portion of avian diversity in most Amazonian and Atlantic forests, with as many as 40 species recorded at a single site (Terborgh *et al*., 1990; Blake, 2007).

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The monophyly of the Thamnophilidae is well supported by both morphology (Ames, 1971; Welsh, 1977) and molecular data (Sibley & Ahlquist, 1990; Irestedt *et al*., 2004; Brumfield *et al*., 2007; Moyle *et al*., 2009; Ohlson *et al*., 2013). Evolutionary relationships within this family were poorly understood until recent molecular studies focusing on intergeneric relationships were completed (Irestedt *et al*., 2004; Brumfield *et al*., 2007; Moyle *et al*., 2009; Bravo *et al*., 2012b; Ohlson *et al*., 2013). These studies have corroborated previous suggestions on the polyphyly of several antbird genera (e.g. Hackett & Rosenberg, 1990; Ridgely & Tudor, 1994; Bates, Hackett & Goerck, 1999; Zimmer & Isler, 2003), and the resurrection or recognition of several new thamnophilid genera in recent years (Bornschein, Reinert & Teixeira, 1995; Isler *et al*., 2006; Isler & Whitney, 2011; Belmonte-Lopes *et al*., 2012; Bravo, Chesser & Brumfield, 2012a; Bravo *et al*., 2012b; Isler, Bravo & Brumfield, 2013). Monophyly of other genera remains to be assessed. The genus *Cercomacra*, the subject of this study, has also been suggested to be non-monophyletic (Zimmer & Isler, 2003).

Cercomacra includes medium-sized birds generally with black, grey or brownish plumage. Males can be distinguished from those of most other Thamnophilid genera by possessing a combination of uniform black or grey plumage, relatively long tails, and small white dots in the greater wing coverts and sometimes at the tips of the rectrices. As with other speciose Thamnophilid genera, *Cercomacra* represents a taxonomically difficult group for defining species limits because of similarity in plumage coloration among populations and species (Bierregaard, Cohn-Haft & Stotz, 1997; Zimmer & Isler, 2003). Proof of this is the recent discovery of two cryptic species overlooked by traditional taxonomy (*laeta* and *parkeri*; Bierregaard *et al*., 1997; Graves, 1997). Males, in general, look very similar to one another while female plumage may vary considerably, a trend called 'heterogyny' (Hellmayr, 1929). Thus, females exhibit the majority of plumage characters one may use to assess relationships within the genus based on morphology (Fitzpatrick & Willard, 1990; Silva, 1992).

As currently defined, *Cercomacra* contains 12 species and 20 subspecies of mid-sized insectivorous antbirds found throughout the continental Neotropics (Peters, 1951; Ridgely & Tudor, 1994; Stotz *et al*., 1996; Bierregaard *et al*., 1997; Graves, 1997; Zimmer & Isler, 2003) (Fig. 1). They occur in forest understorey and borders of lowland and montane humid forest, secondary woodlands, deciduous and gallery woodlands, bamboo thickets, and shrubby clearings in tropical lowlands from Paraguay to Mexico (Ridgely & Tudor, 1994), with highest diversity in Amazonia. A set of species occurs in drier gallery forests or other marginal habitats around the Amazonian periphery (Fitzpatrick & Willard, 1990; Silva, 1992; Ridgely & Tudor, 1994) following a circum-Amazonian distribution (Remsen *et al*., 1991) (Fig. 1A).

To date, no study has formally addressed the relationships of all members of *Cercomacra*, although some studies have partially examined relationships within the genus (Fig. 2), and all were done before *laeta* and *parkeri* were described. Based on comparisons of female plumage patterns and vocalizations, Fitzpatrick & Willard (1990) suggested two species groups, '*tyrannina*' (*tyrannina*, *serva*, *nigrescens*, *brasiliana*) and '*nigricans*' (*nigricans*, *carbonaria*, *ferdinandi*, *melanaria*, *manu*), and left *cinerascens* in an undetermined position. They suggested *C. brasiliana*, from the Atlantic Forest, to belong in the '*tyrannina*' group based on female plumage coloration,

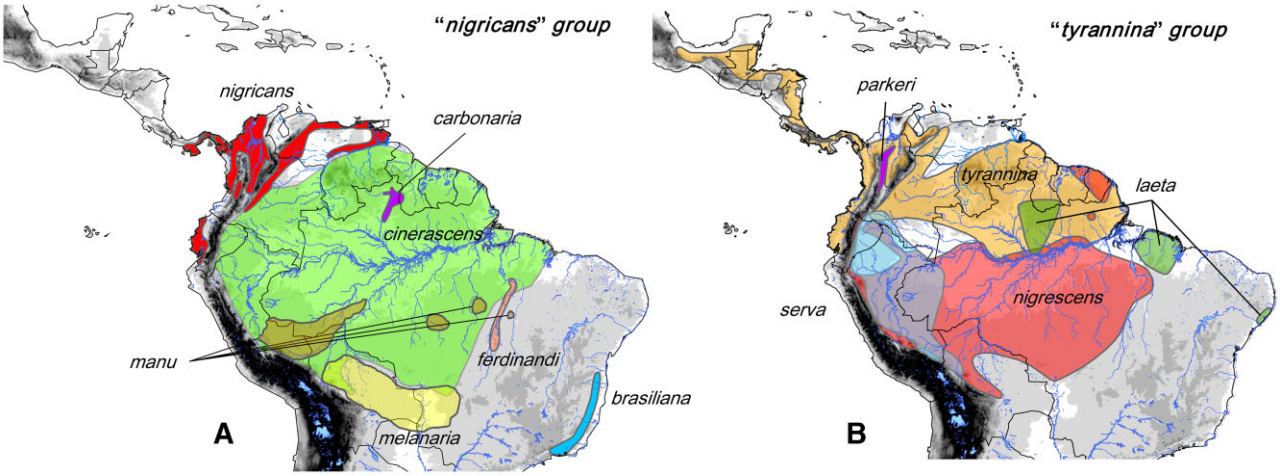

Figure 1. Maps showing current distribution of *Cercomacra* lineages.

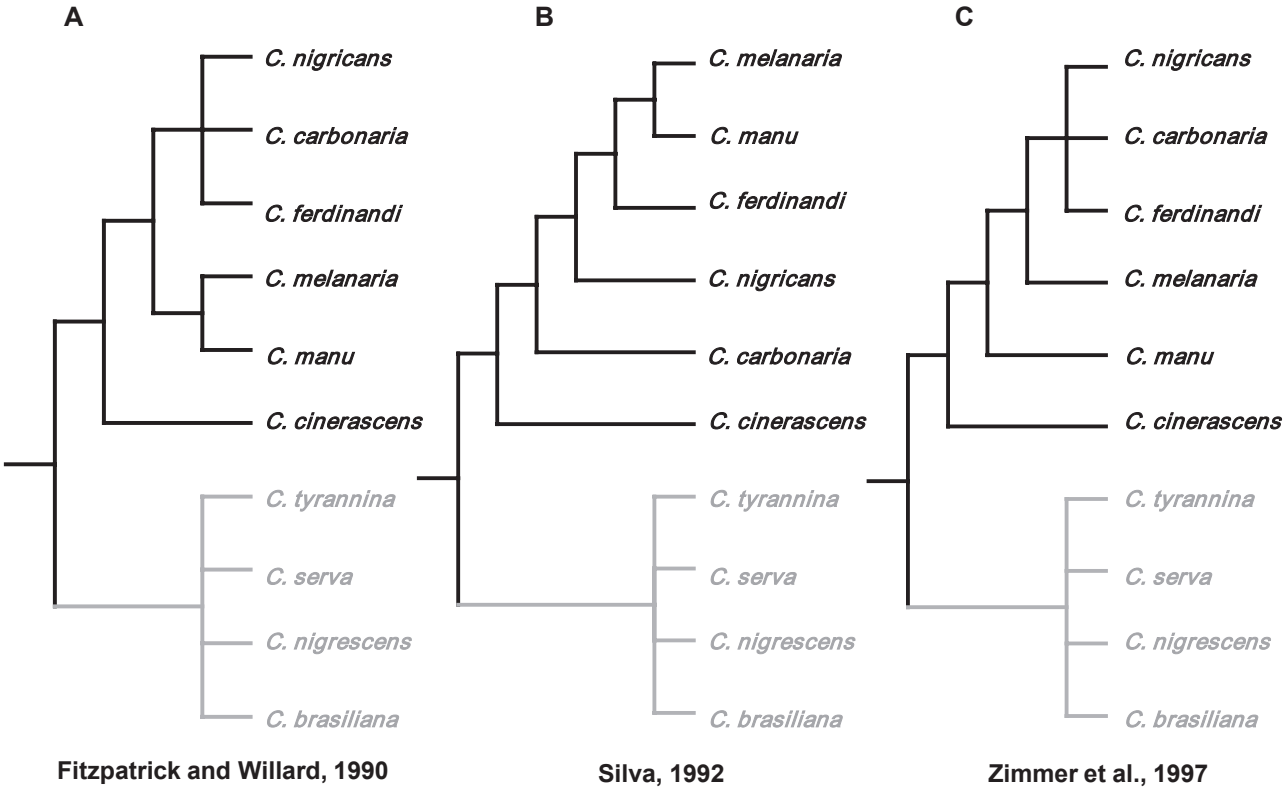

Figure 2. Hypotheses of relationships for the *Cercomacra* '*nigricans*' group: A, Fitzpatrick & Willard (1990); B, Silva (1992); C, Zimmer *et al*. (1997).

but vocalizations of this species were not known. Within the '*nigricans*' group, they suggested a close relationship between *melanaria* and *manu*, and a group formed by *nigricans*, *carbonaria*, and *ferdinandi*. *Cercomacra cinerascens* was suggested to be close to the '*nigricans*' group, but relationships within the '*tyrannina*' group were not suggested (Fig. 2A). A phylogenetic analysis of the '*nigricans*' group based on a small set of plumage and vocal characters suggested that this group is monophyletic, and that *C. cinerascens* is sister to this group (Silva, 1992; Fig. 2B). In contrast to Fitzpatrick and Willard's hypothesis, Silva did not find *nigricans*, *ferdinandi*, and *carbonaria* to be closely related, but recovered *manu* and *melanaria* as sister taxa. Silva's (1992) coding of characters for the '*nigricans*' group has been questioned especially with respect to the inferred relationship between *melanaria* and *manu*. Zimmer, Whittaker & Stotz (1997) suggested that characters that support this relationship (i.e. similar female plumages and narrower white tips in rectrices of both sexes) might be ancestral, and proposed that *melanaria* was sister to a group formed by *nigricans*, *carbonaria*, and *ferdinandi*, and that *manu* was sister to this clade (Fig. 2C). In sum, differences among existing phylogenetic hypotheses are related to the placement of *manu* and the existence of a *nigricans–carbonaria–ferdinandi* clade. Relationships within the '*tyrannina*' group have not been thoroughly assessed and the group is now thought to include the newly described *C. laeta* (Bierregaard *et al*., 1997) and *C. parkeri* (Graves, 1997). It has been suggested that *C. brasiliana* is related to *C. cinerascens* based on male plumage similarities (Cory & Hellmayr, 1924), but similarities in female plumage coloration and ecology suggest a relationship to the '*tyrannina*' group (Fitzpatrick & Willard, 1990; Ridgely & Tudor, 1994), and vocalizations suggest it to be closer to the '*nigricans*' group together with *cinerascens* (Zimmer & Isler, 2003).

The monophyly of *Cercomacra* has been questioned on the basis of differences in nests and vocalizations between the '*nigricans*' and '*tyrannina*' groups, suggesting that morphological characters used to unite these antbirds in *Cercomacra* might be convergent (Zimmer & Isler, 2003). In this study, we test the monophyly of *Cercomacra* using phylogenetic analyses of mitochondrial and nuclear data for all species and suitable outgroups. The results show that the traditional *Cercomacra* is not monophyletic and is composed of divergent clades, requiring a formal description and designation of a new genus.

MATERIAL AND METHODS

Taxon sampling and DNA sequencing

Our taxon sampling for *Cercomacra* included 20 individuals representing all 12 traditionally recognized species (Appendix). We sequenced 13 individuals, representing ten *Cercomacra* taxa and three thamnophilid outgroups (*Cymbilaimus*, *Sciaphylax*, *Sakesphorus*) (Appendix). The other ten *Cercomacra* sequences came from our previous work on thamnophilid relationships (Brumfield *et al*., 2007; Gomez *et al*., 2010) (Appendix). To examine the monophyly of *Cercomacra*, we also included published sequences of 29 of the 48 recognized thamnophilid genera (Irestedt *et al*., 2004; Brumfield *et al*., 2007; Moyle *et al*., 2009; Ohlson *et al*., 2013; Remsen *et al*., 2013) and three non-thamnophilid outgroups (Appendix).

We followed standard methods for DNA extraction, PCR and DNA sequencing for three mitochondrial gene regions, NADH dehydrogenase subunit 2 (*ND2*), NADH dehydrogenase subunit 3 (*ND3*), and cytochrome *b* (*CYTB*); and one nuclear intron, β-fibrinogen intron 5 (*FIB5*) (for detailed description of the methods, see Supporting Information File S1). All sequences were deposited in GenBank (Appendix).

Mitochondrial sequences were aligned to the *ND2*, *ND3*, and *CYTB* sequences of chicken (Desjardins & Morais, 1990) using Sequencher (version 4.1; Gene Codes) and checked by eye. *FIB5* sequences were aligned with each other and checked by eye to identify gap locations in the intron sequences and to find areas of ambiguous alignments in the nuclear data set (as in Brumfield *et al*., 2007).

Phylogenetic analyses

We conducted phylogenetic analyses using Bayesian inference (BI) and maximum-likelihood (ML) methods. Prior to the analysis, we determined the best-fit substitution model for each data partition setting with jModelTest (Posada, 2008) according to the Akaike information criterion (AIC). We did this for the concatenated and separate data sets, and for 17 different partitions of the data based on gene regions and codon positions (data not shown).

We performed BI analyses (Rannala & Yang, 1996; Yang & Rannala, 1997) using MrBayes 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist, Huelsenbeck & Teslenko, 2011). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) sampling was performed, depending on the analysis, with one cold and three or five incrementally heated chains, starting from a random tree; chains were run for ten million generations using the default temperature parameter and default priors as starting values for the model parameters. Trees were sampled every 100th generation. Bayesian posterior probabilities were obtained from the 50% majority-rule consensus of all trees retained after a 10% burn-in. Posterior probability values were considered statistically significant when $P \geq 0.95$. Every analysis was repeated twice (each starting from different, randomly chosen trees) to check for appropriate mixing of MCMCMC sampling. Independent analyses were considered to have converged if their log-likelihood values approached similar mean values. Finally, visual comparisons of the posterior probabilities of the independent runs were done to ensure congruence of the analyses.

We performed ML searches in Garli 2.0 (Zwickl, 2006). Support for the tree was examined using 100 bootstrap replicates (Felsenstein, 1985). Parameters for each of the four genes and the combined data sets were estimated from the ML tree using PAUP*, version 4.0b10 (Swofford, 2002).

For both BI and ML inference, we performed five independent analyses of the concatenated data using different partitioned model settings. The best partitioning strategy was selected based on Bayes factors (Kass & Raftery, 1995; Nylander *et al*., 2004) for BI analysis and AIC for ML. We also performed BI and ML analyses of each mitochondrial gene data set with codon positions in each gene treated as independent partitions. For the *FIB5* analysis, we used a single-partition setting, and combined all mitochondrial genes in a single dataset using a three-model partition setting.

Prior to undertaking concatenated phylogenetic analyses, we used the incongruence length difference (ILD) test (Farris *et al*., 1995a, b) implemented in PAUP*, and an assessment of topological incongruences (see below) to search for conflicting phylogenetic signal among individual partitions and between the mtDNA and *FIB5* data sets.

Congruence among major data partitions and phylogenetic methods

We examined congruence between major data partitions (mitochondrial vs. nuclear intron) by inspecting posterior probabilities ≥ 0.95 and bootstrap values ≥ 70% resulting from the separate BI and ML analyses (Mason-Gamer & Kellog, 1996). We considered nodes with posterior probabilities ≥ 0.95 and/or bootstrap support ≥ 70% supporting different phylogenetic relationships for different partitions as a potential incongruence between partitions (Hillis & Bull, 1993).

Test of monophyly

We used a likelihood-based test using parametric bootstrapping and an a posteriori significance test

(SOWH test; Goldman, Anderson & Rodrigo, 2000) to test for the monophyly of *Cercomacra*. The SOWH test evaluates the significance of the differences between the ML tree (which recovered *Cercomacra* as polyphyletic, see below) and a constraint tree forcing the genus to be monophyletic. We used the program Seq-Gen v1.3.3 (Rambaut & Grassly, 1997) to produce a null distribution using a resampling/reanalysis approach, accomplished by simulating 100 sequence alignments under the null topology (i.e. the constraint tree); we then calculated the likelihood scores of the constraint and ML topology given the simulated alignments in PAUP*, Due to computational constraints, we used a reduced set of taxa ($N = 18$) including all studied traditional species of *Cercomacra* and selected outgroups for the SOWH test.

Estimating divergence times

We used an uncorrelated lognormal relaxed-clock model implemented in the program BEAST (Drummond *et al*., 2012) to estimate divergence times in *Cercomacra*. The analysis was conducted using the mitochondrial data partitions (*ND2*, *ND3*, and *CYTB*), each with individual models of molecular evolution chosen by jModelTest. To calibrate the tree, we used the *CYTB* substitution rate of 2.1% sequence divergence per million years (0.0105 substitutions site^{-1} lineage^{-1} Mya^{-1}; Weir & Schluter, 2008; Weir, Bermingham & Schluter, 2009). We linked the tree model and left the clock and site models unlinked and used a Yule tree prior. Two independent runs of ten million generations were performed, sampling one tree in every 1000 in BEAST 1.7.2. Node posterior probabilities were computed across the sampled trees after a 10% burn-in. We examined marginal probabilities of all samples in Tracer 1.5 (Rambaut & Drummond, 2007) to verify an effective sample size (ESS) exceeding 200 for all parameters. Intervals of divergence times were associated with their respective geological time periods following Gradstein *et al*. (2004).

RESULTS AND DISCUSSION

Data characteristics

The final alignment of the combined mitochondrial and nuclear intron data totalled 3018 bp (mtDNA = 2437 bp; *FIB5* = 581 bp) (Table S1). Within *Cercomacra*, the length of the nuclear sequences showed marked differences between two groups corresponding to the '*nigricans*' group (540–541 bp, seven species, including *cinerascens* and *brasiliana*) and the '*tyrannina*' group (547–552 bp, five species). In outgroups, the length of the nuclear sequences varied from 545 bp in *Liosceles thoracicus* to 564 bp in *Euchrepomis humeralis*. From the aligned sequences we found a total of 36 indel regions that varied from 1 to 13 bp. Although we found no obvious regions of ambiguous alignment in this data set (and therefore we treated indels as missing data in the phylogenetic analyses), a visual examination of the indels showed that members of the '*nigricans*' group present an 11-bp deletion at position 135, which is not found in members of the '*tyrannina*' group. Within this later group, we found a 3-bp deletion at position 273 that was present in *serva*, *tyrannina*, *nigrescens*, and *parkeri*, but not in *laeta*.

Although limited by our taxon sampling, our estimates of intraspecific sequence divergence suggest significant genetic structure within two species in the '*nigricans*' group (*cinerascens* and *manu*) and four species in the '*tyrannina*' group (*nigrescens*, *tyrannina*, *serva*, and *laeta*). Thus, some of these traditional species may constitute species complexes containing geographical structure that needs more study (Table S2). A full report of data characteristics and DNA sequence variation between and within study taxa is available in Supporting Information File S1).

Phylogenetic analyses

Concatenated analyses: In the BI analyses, visual comparisons of tree log-likelihoods and Bayes factors of the runs of different data partition model settings found that the ten-partition model had the best fit to the data. A four-partition model performed significantly better than the three-partition model, the four-partition model with unlinked parameters, and the single-partition model including all data, but was outperformed by the ten-partition model (Table 1). The BI majority rule tree of the best model recovered 14 nodes that uncover *Cercomacra* relationships (Fig. 3, nodes 1–14), with 93% of them having ≥ 0.95 posterior probability support. In the ML analyses, visual comparisons of tree log-likelihoods and the AIC scores of the runs of different data partition models found that the single-partition model had the best fit to the data (Table S3). The ML tree had 86% similarity in nodal congruence to the BI tree. The ML tree recovered 11 nodes (excluding outgroup taxa), 55% of which had ≥ 70% bootstrap support. Differences with the BI tree were due to five highly supported nodes (BP ≥ 0.95) on the Bayesian tree that were not found on the ML tree, and three poorly supported nodes (< 70%) on the ML tree not found on the BI tree.

Separate analyses: With the exception of *ND3* (41.4%), the other Bayesian mitochondrial gene trees (Figs S2–S4, Table S1) recovered either higher (73%, *ND2*)

Table 1. Summary of Bayes factor tests showing the effects of different data partitions on model likelihood

Model* (number of partitions)	1	2	3	4	5
1: Single partition (1)	0				
2: 1st2nd*mtDNA*, 3rd*mtDNA*, *FIB5* (3)	−3133.79†	0			
3: 1st*mtDNA*, 2nd*mtDNA*, 3rd*mtDNA*, *FIB5* (4)	−3457.59	−323.81	0		
4: *ND2*, *ND3*, *CYTB*, *FIB5* (4)	−1097.17	+2036.62	+2360.43	0	
5: 1st*ND2*, 2nd*ND2*, 3rd*ND2*, 1st*ND3*, 2nd*ND3*, 3rd*ND3*, . . . 1st*CYTB*, 2nd*CYTB*, 3rd*CYTB*, *FIB5* (10)	**−3461.15**	**−327.37**	**−3.56**	**−2363.99**	0

The row models are labelled M_0 and positive values in the cells indicate support for the column model (M_1).
*Commas indicate unlinked parameters among partitions.
†Values are twice the log of the Bayes Factors in the comparison between models M_1 and M_0 ($2\log B_{10}$).

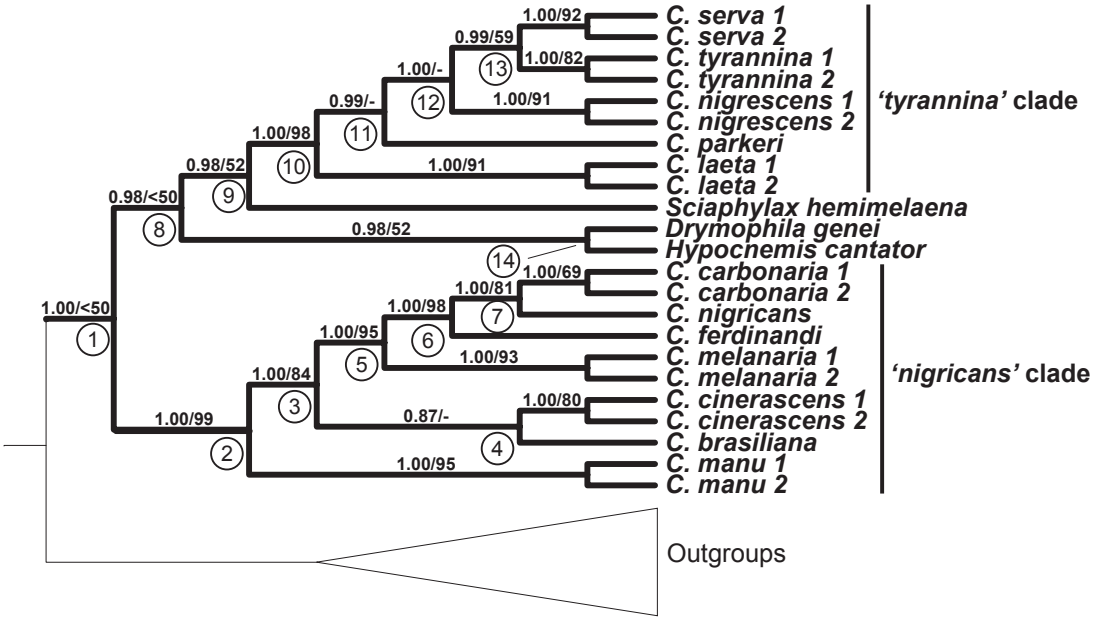

Figure 3. Cladogram of the Bayesian consensus tree of *Cercomacra* from the ten-partition model analysis (−lnL = 37320.48, 1st*ND2*[GTR+G], 2nd*ND2*[TVM+I+G], 3rd*ND2*[HKY+G], 1st*ND3*[SYM+G], 2nd*ND3*[TIM3+I+G], 3rd*ND3*[TIM1+G], 1st*CYTB*[GTR+I+G], 2nd*CYTB*[TIM2+I+G], 3rd*CYTB*[GTR+I+G], *FIB5*[TIM3+G]). Support values correspond to Bayesian posterior probabilities and bootstrap values of the single-partition model ML tree (−lnL = 39246.13, HKY+I+G), respectively. Nodes that uncovered ingroup relationships are numbered 1–14.

or relatively similar (62%, *CYTB*) proportions of supported nodes (posterior probabilities ≥ 0.95) than the *FIB5* (68%) tree (Fig. 4B). The mitochondrial tree (Fig. 4A) had 67% of nodes supported, while the Bayesian concatenated tree had 79% (Fig. 3). *CYTB* and *ND2* trees had the greatest proportion of their nodes congruent with the Bayesian concatenated tree (62 and 60%, respectively). The mitochondrial tree had 72% of congruent nodes and the *FIB5* tree 51%; thus, mitochondrial genes contributed the most to the overall topology of the Bayesian concatenated tree. Topological incongruence between the *FIB5* tree and the mitochondrial tree was found within the '*tyrannina*' group. The incongruence was caused by three highly supported nodes, one in the mitochondrial tree (Node 15, Fig. 4A) and two in the *FIB5* tree (Nodes 11, 12, Fig. 4B).

Based on these results, we used the majority-rule consensus tree and posterior probabilities of the ten-partition Bayesian model to represent the overall topology of the study taxa (Fig. 3), with the exception of three nodes that were involved in the incongruence between the mitochondrial and the *FIB5* data sets (see discussion below).

THE POLYPHYLY OF *CERCOMACRA*

Our BI/ML concatenated tree did not recover *Cercomacra* as monophyletic (Fig. 3). This tree

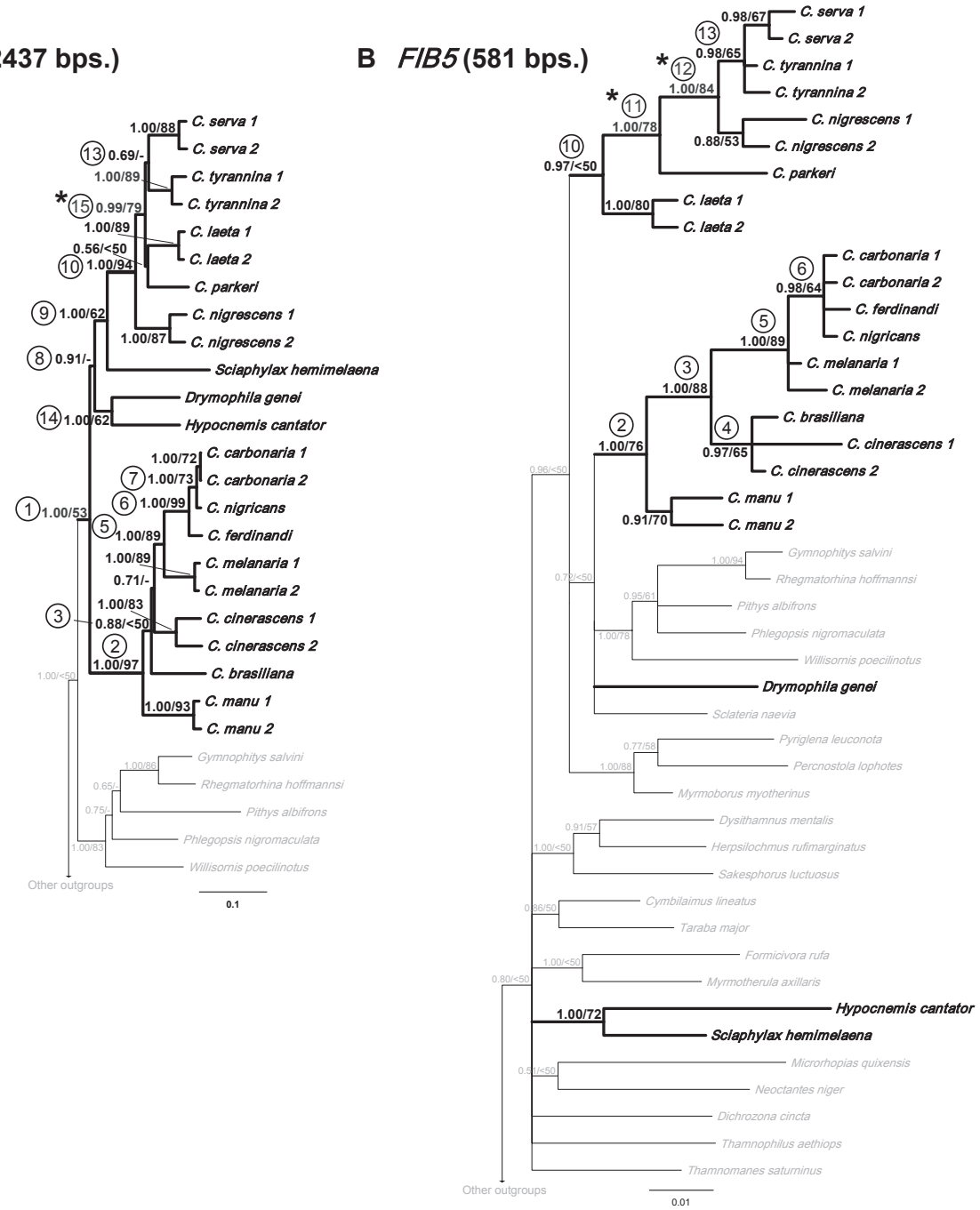

Figure 4. Resulting phylograms of the Bayesian consensus trees of *Cercomacra* from the separate analyses of concatenated mitochondrial (A) and *FIB5* (B) data sets. A, phylogram of Bayesian consensus tree from the concatenated mitochondrial nine-partition model analysis (1st*ND2*[GTR+G], 2nd*ND2*[TVM+I+G], 3rd*ND2*[HKY+G], 1st*ND3*[SYM+G], 2nd*ND3*[TIM3+I+G], 3rd*ND3*[TIM1+G], 1st*CYTB*[GTR+I+G], 2nd*CYTB*[TIM2+I+G], 3rd*CYTB*[GTR+I+G]). B, phylogram of Bayesian consensus tree from the *FIB5* single-partition model analysis (TIM3+G). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively. Numbered nodes represent those also found in the concatenated analysis. Incongruent nodes between the mitochondrial (node 15) and *FIB5* (nodes 11 and 12) trees are marked with asterisks.

recovered two well-supported non-sister groups: (1) the '*nigricans*' clade, including *carbonaria*, *nigricans*, *ferdinandi*, *melanaria*, *cinerascens*, *brasiliana*, and *manu*; and (2) the '*tyrannina*' clade, including *serva*, *tyrannina*, *nigrescens*, *parkeri*, and *laeta*. In the '*nigricans*' clade, *carbonaria* and *nigricans* are sister to *ferdinandi*, and this group is sister to *melanaria*. This whole clade is sister to a weakly supported clade formed by *cinerascens* and *brasiliana*. *Cercomacra manu* is sister to all the other members of the '*nigricans*' clade. In the '*tyrannina*' clade, *laeta* is sister to a clade formed by *parkeri*, *nigrescens*, *serva*, and *tyrannina*. In this latter clade, *serva* and *tyrannina* form a clade sister to *nigrescens*, and this whole clade is sister to *parkeri*. *Sciaphylax* is sister to the '*tyrannina*' clade, forming a group sister relationship to a clade formed by *Drymophila* and *Hypocnemis*. All but one of the 14 nodes that concern '*Cercomacra*' relationships (see Fig. 3) are supported by high Bayesian posterior probabilities. ML bootstrap values, by contrast, were more conservative and only imply high support for six of the 14 nodes (Fig. 3).

Within the '*tyrannina*' group, the mtDNA tree strongly supported *nigrescens* (0.99/79) basal to a clade formed by *laeta*, *parkeri*, *tyrannina*, and *serva* (Fig. 5A), while the *FIB5* tree, which has the same topology as the Bayesian concatenated tree, strongly supported *laeta* (1.00/78) basal to a clade formed by *parkeri*, *nigrescens*, *tyrannina*, and *serva* (Fig. 5B). These incongruent placements may not be related to saturation present in the mtDNA, because the levels of genetic divergence observed within the *tyrannina* clade [8.3 ± 0.4% (1.8–10.7)] were below the range of saturated positions (see Fig. S1). An additional examination of this node showed that the observed incongruence was caused by four *FIB5* substitutions supporting the *FIB5* topology (Fig. 5B) and no *FIB5* changes supporting the alternative mtDNA topology (Fig. 5A). The mitochondrial data supported the mtDNA topology with 53 substitutions and the *FIB5* topology with 29 substitutions (Fig. 5). We found the substitutions supporting these alternative topologies to be evenly distributed throughout the studied sequences, and thus it is unlikely that the mitochondrial and nuclear characters supporting either topology are the product of a particular mitochondrial or nuclear region of high mutation rate. The observed incongruence between markers supporting a different topology could be influenced by short internodes separating *laeta*, *parkeri*, *serva*, and *tyrannina* (see Fig. 4), as well as the slower evolutionary rate and smaller total number of characters of the *FIB5* compared with the mitochondrial genes. Thus, we suggest that the mitochondrial tree must represent the correct basal split within this group.

The results of our BI/ML concatenated analyses show that *Cercomacra*, as traditionally defined, is polyphyletic. Differences in log-likelihoods between the ML tree and the constraint tree in which

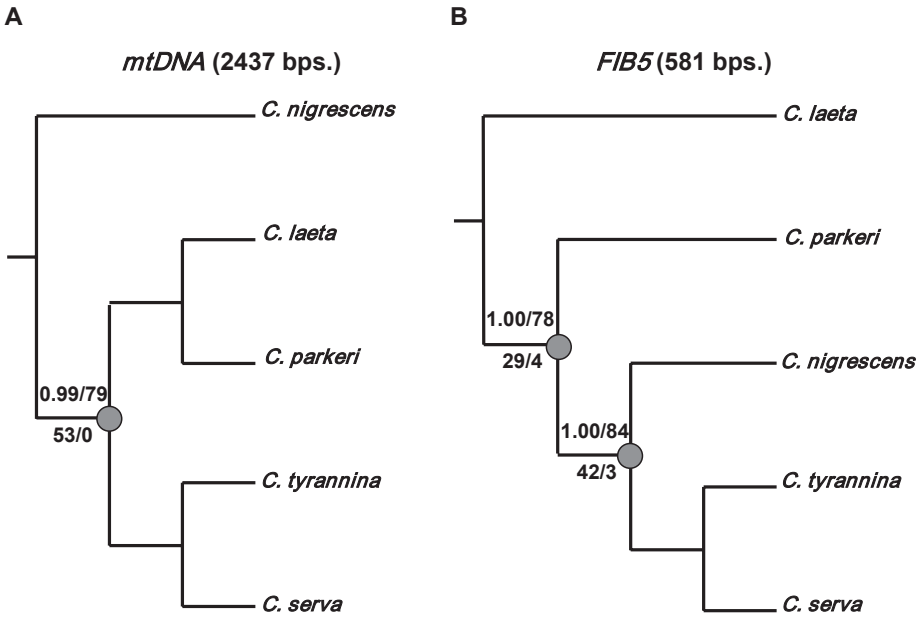

Figure 5. Trees showing incongruent topologies within the '*tyrannina*' clade. The number of mitochondrial and nuclear substitutions supporting those topologies is showed below the branches. Numbers above the branches represent Bayesian posterior probabilities and maximum-likelihood bootstraps.

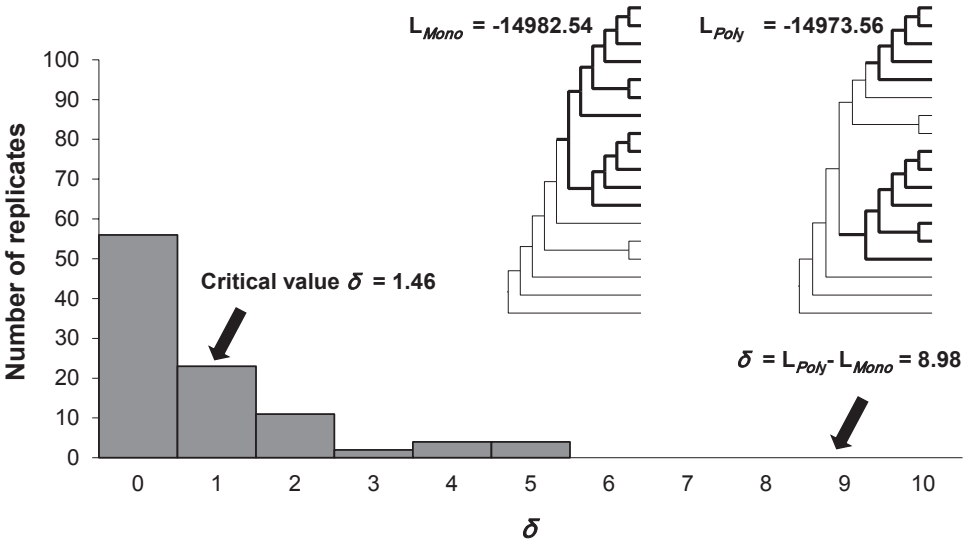

Figure 6. Distribution of the SOWH-test statistic generated by parametric bootstrapping of 100 replicates of the congruent mitochondrial sequence data set using a *Cercomacra*-monophyletic constraint tree as the model tree. The critical value that must be exceeded for a significant result at the 5% level is indicated.

Cercomacra was forced to be monophyletic were statistically significant (SOWH test, $P \leq 0.05$) (Fig. 6).

Morphological, behavioural, and ecological differences between the '*nigricans*' and '*tyrannina*' clades

The non-monophyly of *Cercomacra* is consistent with some plumage, behavioural, and ecological differences between these two clades. Regarding plumage, the species in the '*tyrannina*' clade lack, in both sexes, the conspicuous white tips on the rectrices present in all species of the '*nigricans*' clade (Zimmer & Isler, 2003). Also, females of the '*tyrannina*' clade are predominantly warm buffy-brown or orange buff, whereas females of the '*nigricans*' clade are grey to olive-grey except for *C. cinerascens* in which females are dull greyish brown. Vocal differences among species of the '*nigricans*' and '*tyrannina*' clades are well known. Species in the '*nigricans*' clade ('croakers') engage in complex duets in which female vocal cues are given during the course of the male's loudsong, causing the male to change its vocalization and to begin a synchronized duet (with the exceptions of *cinerascens* and *brasiliana* that perform a more imperfectly synchronized duet). Among the species in the '*tyrannina*' clade ('whistlers'), males and females have very distinctive loudsongs that overlap in timing of delivery, but the female loudsongs start while males are singing (Zimmer & Isler, 2003). Differences in nest architecture also give support for these clades: species in the '*tyrannina*' clade for which nest data are available all build deep pouch-shaped nests with oblique entrances, whereas species in the '*nigricans*' clade build cup-nests with horizontal entrances, with the exception of *C. manu* which builds a pouch-type nest (Kratter, 1998; Zimmer & Isler, 2003; Batista De Pinho *et al.*, 2006). Species in the '*nigricans*' clade are found mostly occupying the midstory to canopy strata of tropical evergreen interior forest, forest edges, and mid-canopy vine-tangles, whereas those from the '*tyrannina*' clade are mostly inhabitants of the understory of forest edge and secondary growth (Stotz *et al.*, 1996; Zimmer & Isler, 2003).

Nomenclature and description of a new genus

Cercomacra, as traditionally defined, has a complex nomenclatural history. Through the years, its species were included in different genera, including *Formicivora* and *Pyriglena*, until Sclater (1858) unified them under *Cercomacra*. When describing this new genus, Sclater (1858: 244), used specimens from Rio de Janeiro that were previously misidentified as *Myrmothera caerulescens* Vieillot, 1817 by Ménétriés (1835, who changed the name to *Formicivora caerulescens*). Additionally, among the specimens that Sclater (1890) identified as *Cercomacra caerulescens* there were specimens from south-eastern Brazil, as well as Pará. Because no known species of *Cercomacra* occurs both in south-eastern Brazil and in Pará, it can be deduced that Sclater's series included more than one species. Sclater's use of the name *Myrmothera caerulescens* was incorrect because it referred to a different taxon (possibly *Willisornis poecilinotus* Cabanis, 1847). Later, Hellmayr (1905) pointed out

that specimens of *Cercomacra caerulescens* (Sclater, 1858) did not match those of *Myrmothera caerulescens* Vieillot, 1817, and proposed a new name for Sclater's species, *Cercomacra brasiliana*, listing six specimens from south-eastern Brazil as syntypes. A direct implication of Hellmayr introducing the name *C. brasiliana* as a *nomen novum* for *C. caerulescens* Sclater, 1858 is that the type series of *Cercomacra brasiliana* is the series used by Sclater (1890: 264) to designate his *C. caerulescens*, and not the specimens Hellmayr (1905) pointed out later. This complex nomenclatural history involves at least four species, as well as the actual definition of the genus *Cercomacra*, a problem that will be fully addressed in a future publication (M. Raposo *et al*., in preparation). Here we opt to adopt the proposition of Cory & Hellmayr (1924, p. 213), which considers *C. brasiliana* as the type species of *Cercomacra* and, simultaneously, we consider that the name is applicable to the south-eastern Brazilian populations of this genus, first called *Formicivora caerulescens* Ménétriés, 1835 and then *Cercomacra caerulescens* Sclater, 1858.

Based on the results of the phylogenetic analyses, the genus *Cercomacra* is therefore applicable to the species: *Cercomacra brasiliana* Hellmayr, 1905; *Cercomacra nigricans* Sclater 1858; *Cercomacra carbonaria* Sclater & Salvin, 1873; *Cercomacra cinerascens* (Sclater, 1857); *Cercomacra ferdinandi* Snethlage, 1928, *Cercomacra melanaria* (Ménétriés, 1835), and *Cercomacra manu* Fitzpatrick and Willard, 1990.

Because the group of species referred to as the '*tyrannina*' clade does not have an available name, we erect a new genus that recognizes the monophyly and distinct nature of this group.

CERCOMACROIDES J. G. TELLO & M. A. RAPOSO, GEN. NOV.

Type species: Cercomacroides tyrannina (Sclater, 1855), comb. nov., Dusky Antbird (= *Cercomacra tyrannina* [Sclater], 1855).

Other included species: Cercomacroides laeta (Todd, 1920), comb. nov., Willis's antbird; *Cercomacroides serva* (Sclater, 1858), comb. nov., black antbird; *Cercomacroides nigrescens* (Cabanis & Heine, 1859), comb. nov., blackish antbird; *Cercomacroides parkeri* (Graves, 1997), comb. nov., Parker's antbird.

Diagnosis: Comparisons in the diagnosis are only between *Cercomacroides* and *Cercomacra* because a previous study (Isler *et al*., 2013) has already reported comparisons between the *tyrannina* clade (= *Cercomacroides*) and the other genera (*Sciaphylax*, *Drymophila*, and *Hypocnemis*) in the larger Thamnophilid clade (Fig. 3). *Cercomacroides* can be distinguished from *Cercomacra* by the lack of conspicuous white tips on the rectrices of both sexes; by the predominantly warm buffy-brown or orange buff plumage in females; by the whistling loudsongs and non-synchronized vocal duets; and by building deep pouch-shaped nests with oblique entrances.

Etymology: The Latin suffix *-oides*, taken from ancient Greek 'eidos' means 'having the likeness of'. Our choice of the name *Cercomacroides* is an allusion to the great shape and plumage similarity among the species of *Cercomacroides* and those of the genus *Cercomacra*, probably as a result of convergence.

We recommend the following placement and provisional classification of *Cercomacra* and *Cercomacroides*, based on our phylogeny and the proposed classification of Furnariides by Moyle *et al*. (2009) and Ohlson *et al*. (2013):

FAMILY Thamnophilidae
TRIBE Pithyini
Cercomacra
Cercomacroides, *Sciaphylax*
Drymophila, *Hypocnemis*

CERCOMACRA SCLATER, 1858

Cercomacra manu (Fitzpatrick & Willard, 1990)
Cercomacra brasiliana (Hellmayr, 1905), type of *Cercomacra*
Cercomacra cinerascens (Sclater, 1857)
Cercomacra melanaria (Ménétriés, 1835)
Cercomacra ferdinandi (Snethlage, 1928)
Cercomacra carbonaria (Sclater & Salvin, 1873)
Cercomacra nigricans (Sclater, 1858)

CERCOMACROIDES GEN. NOV.

Cercomacroides nigrescens (Cabanis & Heine, 1859)
Cercomacroides laeta (Todd, 1920)
Cercomacroides parkeri (Graves, 1997)
Cercomacroides tyrannina (Sclater, 1855), type of Cercomacroides
Cercomacroides serva (Sclater, 1858)

RELATIONSHIPS WITHIN *CERCOMACRA*

Cercomacra comprises *manu*, *brasiliana*, *cinerascens*, *melanaria*, *ferdinandi*, *carbonaria*, and *nigricans* (Fig. 3). *Cercomacra manu* is sister to the rest of *Cercomacra*, which comprises two clades: one clade formed by the circum-Amazonian taxa (*melanaria*, *ferdinandi*, *carbonaria*, and *nigricans*), in which *carbonaria* and *nigricans* are sister to *ferdinandi*, and then to *melanaria*; and a second clade formed by the Amazonian *cinerascens* and the south-eastern

Atlantic Forest *brasiliana*. All nodes received high posterior probability and ML bootstrap support, with the exception of the node uniting *cinerascens* and *brasiliana* (Fig. 3). Resolution of this latter node has important biogeographical implications (see below) and needs to be investigated further. Vocal similarities between *cinerascens* and the circum-Amazonian taxa support a close relationship between these taxa (Fitzpatrick & Willard, 1990; Zimmer *et al*., 1997; Isler & Whitney, 2002), as supported (albeit weakly) by the mtDNA tree (Fig. 4A).

Contrasting with previous hypotheses (Fig. 2), our molecular analyses found that the '*nigricans*' group, as delimited by Fitzpatrick & Willard (1990), Silva (1992), or Zimmer *et al*. (1997), does not constitute a natural group, because *brasiliana* and *cinerascens* are embedded within this clade (Fig. 3). Similarity in vocalizations, i.e. a two-element call of males and a single element in the female call during the duet, supports the inclusion of *cinerascens* and *brasiliana* within *Cercomacra senso stricto* (Vielliard, 1995; Isler & Whitney, 2002; Zimmer & Isler, 2003). The phylogenetic results also agree with the previous suggestion of a close relationship between *carbonaria*, *nigricans*, and *ferdinandi* (Fitzpatrick & Willard, 1990; Zimmer *et al*., 1997; Fig. 2A, C). The species in this subclade possess plumage (heavy streaking on throat of females) and vocal (male–female duet song pattern) similarities that support their close relationship, particularly between *nigricans* and *carbonaria* (Fitzpatrick & Willard, 1990; Zimmer *et al*., 1997; Isler & Whitney, 2002; Zimmer & Isler, 2003). Our results confirm Zimmer *et al*.'s (1997) conclusion that characters suggesting a close relationship between *melanaria* and *manu* (Fitzpatrick & Willard, 1990; Silva, 1992), i.e. the overall similarity in female plumages, are probably due to sharing ancestral or convergent features within the group.

Relationships within *Cercomacroides*

The new genus *Cercomacroides* comprises *nigrescens*, *laeta*, *parkeri*, *tyrannina*, and *serva*. In the concatenated tree, all internal nodes within *Cercomacroides* received high posterior probability support, but low or no ML bootstrap support (Fig. 3). An incongruent signal between the mitochondrial and nuclear markers was uncovered in this group, and the concatenated tree was biased toward the *FIB5* signal (see discussion above and Figs 3–5). The main difference between these two topologies is regarding the identity of the taxon sister to the rest of the group: *nigrescens* in the mtDNA tree, and *laeta* in the *FIB5* tree (Fig. 5). Both major data sets supported a close relationship between *serva* and *tyrannina* (although support in the mitochondrial tree was low; Fig. 4A), which was not expected due to the great plumage similarity between *tyrannina* and *parkeri* (Graves, 1997). Overall similarities in male and female vocalizations (based on the analysis of vocalizations from Isler & Whitney, 2002) and plumage coloration (Graves, 1997; Zimmer & Isler, 2003) suggest that *parkeri* is closer to *tyrannina* and *serva* than to *laeta* or *nigrescens*, but do not provide clear evidence for the phylogenetic placement of *laeta* and *nigrescens*. Full resolution of the internal relationships within *Cercomacroides* may require the addition of more nuclear markers.

Divergence estimates of *Cercomacra* and *Cercomacroides*

Posterior rate estimates (parameter 'meanRate' in BEAST) ranged from 0.30 to 0.42% s s^{-1} Mya^{-1} for *FIB5*, 1.92 to 2.16% for *CYTB*, 1.82 to 2.40% for *ND3*, and 2.24 to 2.86% for *ND2*. According to this tree (Fig. 7), the age of the roots of *Cercomacra* and *Cercomacroides* clades ranged from the late Miocene through the early Pliocene between 9.3 and 4.2 Mya [*Cercomacra*, mean = 6.7 Mya (9.3–4.5 Mya); *Cercomacroides*, mean = 6.2 Mya (8.6–4.2 Mya)]. Subsequent major splits within the *Cercomacra* and *Cercomacroides* clades all are estimated to have occurred between the Late Miocene and Late Pleistocene (9.3–0.3 Mya within *Cercomacra*; and 8.6–3.3 Mya within *Cercomacroides*). The separation of *Cercomacroides* from *Sciaphylax* was estimated to have occurred *c*. 9.6 Mya (13.2–6.4 Mya), and this latter clade separated from the *Hypocnemis–Drymophila* clade *c*. 11.0 Mya (15.0–7.5 Mya). Finally, the *Cercomacroides–Sciaphylax–Hypocnemis–Drymophila* clade separated from *Cercomacra* at approximately 11.6 Mya (15.9–7.9 Mya).

The ancestral *Cercomacra* lineage split from its most recent common ancestor in the mid to late Miocene (see above). *Cercomacra manu*, the taxon diverging first from the rest of the genus, split in the late Miocene to early Pliocene between 9.3 and 4.5 Mya. The phylogenetic position of *brasiliana* and *cinerascens* is not yet resolved. *Cercomacra brasiliana* is either sister to *cinerascens* (Figs 3, 4B) or sister to the *cinerascens*–circum-Amazonian clade (*melanaria*, *ferdinandi*, *carbonaria*, and *nigricans*) (Fig. 4A). Alternatively, it may be sister to the circum-Amazonian clade (although this relationship was not recovered in any of the analyses). Internal branches separating these three major clades are short and divergence of all three occurred within 1 Mya (Figs 4A, 7). The mitochondrial tree suggests that *brasiliana* is sister to the *cinerascens*–circum-Amazonian clade, and that divergence occurred in the late Miocene to early Pliocene between 8.0 and 3.9 Mya. The mitochondrial topology shows that

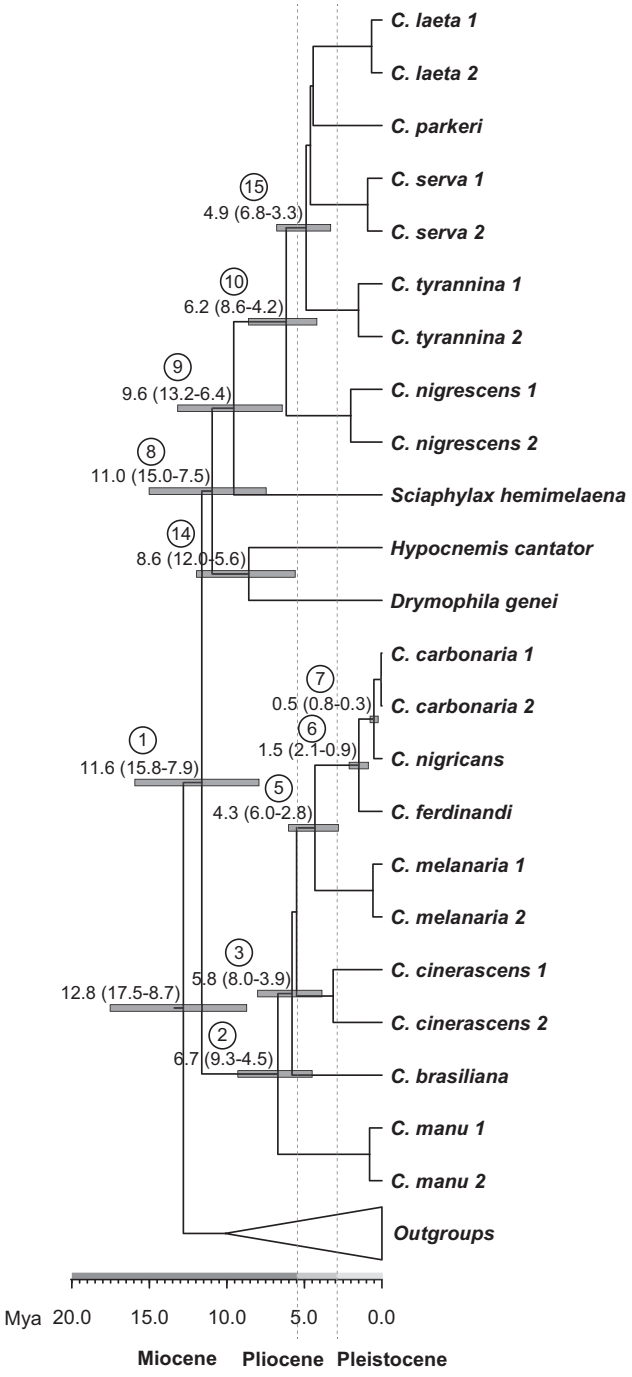

Figure 7. Chronogram of *Cercomacra* and ***Cercomacroides* gen. nov.** indicating divergence time estimates based on Bayesian relaxed clock analysis of the mitochondrial concatenated data. Shaded bars on nodes correspond to the 95% confidence intervals of the time estimates. Scale numbers correspond to millions of years before present. Numbered nodes represent those also found in the concatenated analysis. Node 15 was only found in the mitochondrial tree.

cinerascens is sister to the circum-Amazonian clade, diverging in the late Miocene to early Pliocene between 7.6 and 3.7 Mya. Within the circum-Amazonian clade, the split of *melanaria* from the rest of the taxa took place between 6.0 and 2.8 Mya. Subsequent splits in *Cercomacra* took place in the Pleistocene and included the separation of *ferdinandi* from the *carbonaria–nigricans* clade between 0.9 and 2.1 Mya, and the separation of *carbonaria* and *nigricans* between 0.8 and 0.3 Mya.

The ancestral *Cercomacroides* lineage split from its most recent common ancestor in the middle to late Miocene between 13.2 and 6.4 Mya. The lack of resolution of the internal nodes in the *Cercomacroides* tree due to data incongruence prevents us from determining the order in which internal splits took place. However, the mitochondrial topology suggests that the earliest split took place sometime in the late Miocene to early Pliocene between 8.6 and 4.2 Mya, and involved the basal divergence between *nigrescens* and the *laeta–tyrannina–parkeri–serva* clade. The order of splits that separated these four taxa is unknown, but based on the mitochondrial tree estimates, we can suggest that they took place not far from each other sometime between 6.8 and 3.3 Mya (Fig. 7).

Cercomacra and *Cercomacroides* constitute two independent lineages of similar age distributed in several major areas of endemism (Table S4), whose relationships can provide important insights on the biogeography of the Neotropical lowlands. Both genera originated sometime between the late Miocene and early Pliocene. This range of time, particularly between 3 and 7 Mya, coincides with molecular estimates of the time of origin of several Neotropical avian genera (e.g. Lovette, 2004; Pereira & Baker, 2004; Barker, 2007; Miller *et al*., 2008; Ribas, Miyaki & Cracraft, 2009; Antonelli *et al*., 2010; Patel *et al*., 2011). Diversification in the late Miocene to early Pliocene coincides with a time period of dynamic geomorphological activity in the region (Antonelli *et al*., 2010; Hoorn *et al*., 2010a; Wesselingh *et al*., 2010). During this period, the completion of present-day patterns of river systems and drainage divides in South America began to be achieved (Campbell, Frailey & Romero-Pittman, 2006; Figueiredo *et al*., 2009; Hoorn *et al*., 2010b; Latrubesse *et al*., 2010). A combination of tectonics (Andean uplift) and sea transgressions, due to sea-level rise, led to the formation of structural arches, palaeorivers, and ancient lakes that may have contributed to diversification of biota (Lundberg *et al*., 1998; Hoorn *et al*., 2010a; Wanderley-Filho *et al*., 2010). Diversification during the late Pliocene coincides with a time of strong global cooling and the formation of the first glacial period at the end of the Pliocene (van der Hammen & Hooghiemstra, 2000), with subsequent effects on the vegetation cover, structure, and species composition of the region (Colinvaux *et al*., 1996; Haffer, 1997, Colinvaux & De Oliveira, 2001; Haffer & Prance, 2001; Behling, Bush & Hooghiemstra, 2010). This also coincides with the presence of an extensive wetland system occupying the western Amazonian basin (Klammer, 1984; Frailey, 1988; Marroig & Cerqueira, 1997; Hoorn *et al*., 2010b). The palaeogeographical conditions at that time (arches, river basins, etc.) that start forming at the late Miocene, together with climate fluctuations that characterized the late Pliocene to late Pleistocene, may have contributed to the origination of current Neotropical avian diversity (Haffer, 1997; Aleixo & Rossetti, 2007; Antonelli *et al*., 2010).

All these factors may have played some role in the diversification of *Cercomacra* and *Cercomacroides* lineages. Today, the distributions of members of these two lineages present an interesting contrast to the majority of currently documented biogeographical patterns for Amazonian birds. These birds exhibit a great degree of range overlap that exists within related lineages of different ages. *Cercomacra* includes divergent overlapping Amazonian taxa, including the more restricted *manu* and the widespread Amazonian *cinerascens* along with the circum-Amazonian lineage, one of which (*carbonaria*) has a distribution completely within the range of *cinerascens* (Fig. 1). Ecological differences between these species are significant (e.g. *manu* is a bamboo specialist, *carbonaria* a gallery forest species and *cinerascens* a mid-canopy, vine tangle specialist). The ecological differences between the broadly overlapping members of *Cercomacroides* (*serva* and *nigrescens*; *laeta* and *tyrannina*) are less obvious and offer an interesting system to investigate the co-occurrence of comparatively young and ecologically similar lineages in Amazonia.

CONCLUSIONS

Phylogenetic analyses of mitochondrial and nuclear intron data documented phylogenetic relationships between and among putative *Cercomacra* lineages. The analyses of concatenated and separated data sets identified phylogenetic incongruence between the mitochondrial and nuclear intron data at some intermediate nodes, which are probably caused by the smaller number of nuclear compared with mitochondrial characters, and the presence of short internodes separating those relationships.

Two non-sister clades in putative *Cercomacra* were uncovered by this study and one received a new generic description: (1) *Cercomacra sensu stricto*, formed by *manu*, *brasiliana*, *cinerascens*, *melanaria*, *ferdinandi*, *carbonaria*, and *nigricans*; and (2) *Cercomacroides* gen. nov., formed by *nigrescens*, *laeta*, *parkeri*, *tyrannina*, and *serva*. *Sciaphylax* was sister to *Cercomacroides* and this group was sister to a clade formed by *Drymophila* and *Hypocnemis*. This whole major clade then was sister to *Cercomacra*. Further work is needed to resolve the phylogenetic placement of *brasiliana* and *cinerascens* within *Cercomacra*, and the relationships within *Cercomacroides*.

This study provides an initial historical framework to begin reconstructing the biogeographical history

of these lineages. *Cercomacra* and *Cercomacroides* belong to one of the most specious families in the Neotropics, and thus historical patterns of diversification derived from these genera are potentially representative of the evolutionary history of a good portion of the Neotropical lowland forest avifauna. Both from taxonomic and from biogeographical perspectives, these two genera constitute broadly informative Neotropical case studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

File S1. Supplementary text including materials and methods, results and discussion.

Figure S1. Comparison of uncorrected percentage sequence divergence between mtDNA and *FIB5*. The slope is represented by the regression equation. Black circles represent comparisons within the '*nigricans*' group; light grey circles represent comparisons within the '*tyrannina*' group; grey circles represent comparisons between the '*nigricans*' and '*tyrannina*' groups; and white circles represent comparisons with the outgroups.

Figure S2. Phylogram of Bayesian consensus tree from the *ND2* three-partition model analysis (1st[GTR+G], 2nd[TVM+I+G], 3rd[HKY+G]). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively.

Figure S3. Phylogram of Bayesian consensus tree from the *ND3* three-partition model analysis (1st[SYM+G], 2nd[TIM3+I+G], 3rd[TIM1+G]). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively.

Figure S4. Phylogram of Bayesian consensus tree from the *CYTB* three-partition model analysis (1st[GTR+I+G], 2nd[TIM2+I+G], 3rd[GTR+I+G]). Support values correspond to Bayesian posterior probabilities and ML bootstrap values, respectively.

Table S1. Properties of three mitochondrial genes and one nuclear intron based on maximum-parsimony, maximum-likelihood, and Bayesian inference.

Table S2. Uncorrected pairwise percentage sequence divergence (p) at different taxonomic levels for three mitochondrial genes and one nuclear intron (mean ± SE, range in parentheses).

Table S3. Summary of AIC scores showing the effects of different data partitions on model likelihood.

Table S4. Geographical distribution in major area(s) of endemism for *Cercomacra* and *Cercomacroides* taxa.

APPENDIX

Collection data and voucher information for tissue samples used in this study.

Taxon	Locality	Museum Code[a]	GenBank Accession Numbers[b]
C. brasiliana	Brazil: Rio de Janeiro: Fazenda Bela Vista, Cordeiro, 22° 02′ S, 42° 18′ W, 337 m elev.	MNRJ 44251	HM637230, HM637271, HM637136, HM637183
C. carbonaria 1	Brazil: Rondônia: Fazenda Santa Cecília, E bank Rio Branco, across from Boa Vista.	FMNH 389250	HM637234, HM637276, HM637141, HM637188
C. carbonaria 2	Brazil: Rondônia: Fazenda Santa Cecília, E bank Rio Branco, across from Boa Vista.	FMNH 389251*	KF826071, KF826030, KF826043, KF826057
C. cinerascens (sclateri) 1	Perú: Loreto: 79 km WNW Contamana, 7° 08′ S, 75° 41′ W, 400 m elev.	LSUMNS B28057	HM637229, HM449834, HM637135, HM637182
C. cinerascens (cinerascens) 2	Perú: Loreto: 1 km N Río Napo, 157 km by river NNE Iquitos.	LSUMNS B2859*	KF826072, JQ445275, KF826044, KF826058
C. ferdinandi	Brazil: Tocantins: Parque Estadual do Cantão, 09° 15′ 53″ S, 50° 00′ 39″ W.	MZUSP 79871*	KF826073, KF826031, KF826045, KF826059
C. laeta (sabinoi) 1	Brazil: Pernambuco: Timbaúba.	FMNH 392376	HM637231, HM637272, HM637137, HM637184
C. laeta (waimiri) 2	Brazil: Roraima: Rio Cachorro, 4 km N on Cantá to Confiança Road.	FMNH 389253*	KF826076, KF826034, KF826048, KF826062
C. manu 1	Brazil: Pará: 126 km NW Alta Floresta S bank Rio São Benedito	LSUMNS B35304	HM637236, HM637278, HM637143, HM637190
C. manu 2	Bolivia: Pando: Nicolás Suarez; 12 km by road S of Cobija, 8 km W on road to Mucden.	LSUMNS B9100*	KF826074, KF826032, KF826046, KF826060
C. melanaria 1	Bolivia: El Beni: Laguna Suarez, 5 km sw Trinidad, 230 m elev.	FMNH 334470	HM637235, HM637277, HM637142, HM637189
C. melanaria 2	Paraguay: Alto Paraguay: W bank Río Negro, *ca*. 8 km above mouth, 20° 06′ S, 58° 08′ W.	UKNHM B2995*	KF826075, KF826033, KF826047, KF826061
C. nigrescens (approximans) 1	Brazil: Rondônia: Cachoeira Nazare, W bank Rio Jiparaná, 100 m elev.	FMNH 389848	HM637233, HM637274, HM637139, HM637186
C. nigrescens (fuscicauda) 2	Perú: Loreto: S bank Rio Marañón, along Río Samiria, Estación Biológica Pithecia, Base Tacsha Cocha.	LSUMNS B10351*	KF826077, KF826035, KF826049, KF826063
C. nigricans	Panamá: Darien: Cana on E Slope Cerro Pirre.	LSUMNS B2277	HM637233, HM637275, HM637140, HM637187
C. serva (hypomelaena) 1	Bolivia: Pando: Nicolás Suarez; 12 km by road S of Cobija, 8 km W on road to Mucden.	LSUMNS B9254*	KF826078, KF826036, KF826050, KF826064
C. serva (serva) 2	Ecuador: Jatun Sacha.	STRI EC-CSE1*	KF826079, KF826037, KF826051, KF826065
C. parkeri	Colombia: Antioquia	IAvH-CT 4962	HM637232, HM637273, HM637138, HM637185
C. tyrannina (crepera) 1	Costa Rica: Puntarenas: Río Copey, 4 km E Jaco.	LSUMNS B16079*	KF826080, KF826038, KF826052, KF826066
C. tyrannina (saturatior) 2	Venezuela: Amazonas: Río Mauaca, Base Camp, 120 m elev.	AMNH 18044*	KF826081, KF826039, KF826053, KF826067
Cymbilaimus lineatus	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389850*	KF826082, KF826040, KF826054, KF826068
Dichrozona cincta	Bolivia: La Paz: T.C.O Campamento Araona, 'Palmasola', Rio Manupari.	FMNH 391144	EF639878, EF640010, EF640077, EF639943
Dixiphia mentalis	Mexico: Veracruz.	LSUMNS B18078	DQ294448, DQ294535, DQ294404, DQ294491
Drymophila genei	Brazil: Minas Gerais: Parque Nacional Caparao.	FMNH 432972	EF639879, EF640011, EF640078, EF639944
Dysithamnus mentalis	Brazil: Pernambuco: Serra do Espelho.	FMNH 392443	EF639880, EF640012, EF640079, EF639945

APPENDIX *Continued*

Taxon	Locality	Museum Code[a]	GenBank Accession Numbers[b]
Formicivora rufa	Brazil: Amapá: Amapá, Fazenda Itapoá.	FMNH 391399	EF639881, EF640013, EF640080, EF639946
Gymnophitys salvini	Bolivia: La Paz: Puerto Araona, Río Manupari.	FMNH 391147	EF639884, EF640016, EF640083, EF639949
Herpsilochmus rufimarginatus	Venezuela: Bolivar: Tumeremo, 23 km S.	FMNH 339650	EF639885, EF640017, EF640084, EF639950
Hylopezus berlepschi	Perú: Madre de Dios: Hacienda Amazonia.	FMNH 322345	EF639886, EF640018, EF640085, EF639951
Hypocnemis peruviana	Bolivia: El Beni: Hacienda Los Angeles, 10 km E Riberalta.	FMNH 391136	EF639889, EF640021, EF640088, EF639954
Hypocnemoides maculicauda	Brazil: Pará: Caxiuanã.	FMNH 391414	EF639890, EF640022, EF640089, EF639955
Liosceles thoracicus	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 390080	EF639892, EF640024, EF640091, EF639957
Microrhopias quixensis	Perú: Madre de Dios: Hacienda Amazonia.	FMNH 321993	EF639895, EF640027, EF640094, EF639960
Myrmophylax atrothorax	Perú: Madre de Dios: Hacienda Amazonia.	FMNH 322209	EF639896, EF640028, EF640095, EF639961
Sciaphylax hemimelaena	Perú:Ucuyali:Lower Urubamba: Centro Pucani 10° 40.5′S 73° 32.7′W.	STRI MJM796*	KF826083, KF826041, KF826055, KF826069
Myrmoborus myotherinus	Brazil: Pará: Serra dos Carajás.	FMNH 391406	EF639902, EF640035, EF640102, EF639968
Myrmorchilus strigilatus	Brazil: Sergipe: Canindé do São Francisco, Curituba, Fazenda Mirama.	FMNH 392862	EF639904, EF640037, EF640104, EF639970
Myrmornis torquata	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389880	EF639905, EF640038, EF640105, EF639971
Myrmotherula axillaris	Brazil: Pernambuco: Serra do Espelho.	FMNH 392444	EF639906, EF640039, EF640106, EF639972
Neoctantes niger	Perú: Cuzco: Tono.	FMNH 321806	EF639908, EF640042, EF640109, EF639975
Percnostola lophotes	Perú: Madre de Dios: Moskitania, 13.4 km NNW Atalaya, left bank of Alto Madre de Dios River.	FMNH 433492	EF639909, EF640043, EF640110, EF639976
Phlegopsis nigromaculata	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389842	EF639912, EF640046, EF640113, EF639979
Pithys albifrons	Brazil: Amapá.	FMNH 391430	EF639913, EF640047, EF640114, EF639980
Pygiptila stellaris	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389931	EF639914, EF640048, EF640115, EF639981
Pyriglena leuconota	Bolivia: Santa Cruz: San José-San Ignacio Road, Km 69.	FMNH 334469	EF639915, EF640049, EF640116, EF639982
Rhegmatorhina hoffmannsi	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389933	EF639916, EF640050, EF640117, EF639983
Sakesphorus luctuosus	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389938*	KF826084, KF826042, KF826056, KF826070
Sclateria naevia	Brazil: Amapá.	FMNH 391418	EF639918, EF640052, EF640119, EF639985
Taraba major	Perú: Madre de Dios: Hacienda Amazonia.	FMNH 321773	EF639919, EF640053, EF640120, EF639986
Terenura humeralis	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389942	EF639920, EF640054, EF640121, EF639987
Thamnomanes saturninus	Brazil: Rondônia: Cachoeira Nazaré, W bank Rio Jiparaná, 100 m elev.	FMNH 389947	EF639923, EF640057, EF640124, EF639990

APPENDIX *Continued*

Taxon	Locality	Museum Code[a]	GenBank Accession Numbers[b]
Thamnophilus aethiops	Brazil: Alagoas: Ibateguara, Engenho Coimbra, Usina Serra Grande.	FMNH 399223	EF639924, EF640058, EF640125, EF639991
Willisornis poecilinotus	Bolivia: La Paz: T.C.O Campamento Araona, 'Palmasola', Río Manupari.	FMNH 391148	EF639888, EF640020, EF640087, EF639953

*Indicate sequences added to GenBank for this study.

[a]Museum abbreviations: MNRJ = Museu Nacional da Universidade Federal do Rio de Janeiro; FMNH = Field Museum of Natural History; LSUMNS = Louisiana State University Museum of Natural Science; MZUSP = Museum of Zoology of the University of São Paulo; UKMNH = University of Kansas Museum of Natural History; IAvH-CT = Colección de Tejidos, Instituto Alexander von Humboldt; AMNH = American Museum of Natural History; STRI = Smithsonian Tropical Research Institute.

[b]*BF5*, *ND2*, *ND3*, *CYTB*.